Rhizosphere 8 (2018) 12–26

Contents lists available at ScienceDirect

Rhizosphere

journal homepage: www.elsevier.com/locate/rhisph

Arbuscular mycorrhizal symbiosis in rice: Establishment, environmental control and impact on plant growth and resistance to abiotic stresses

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ARTICLE INFO

Keywords:
Rice
Roots
Arbuscular mycorrhizal fungi (AMF)
Phosphate
Salt
Drought
Breeding

ABSTRACT

Rice is one of the most consumed crop around the globe and its production needs to be increased in a context of climate change and water scarcity. Rice roots, as most land plants, can establish symbiotic association with arbuscular mycorrhizal fungi (AMF). Rice has emerged, in the past decade, as a model to study the molecular determinants of AM symbiosis establishment and functioning, providing insight into potential breeding target to improve the capacity of this crop to interact with AMF. Furthermore, evidences showing the beneficial effects of AMF on rice performance in field conditions and resistance to abiotic stresses in controlled conditions are increasing. In this review, we describe recent discoveries about rice root AMF interactions and collect evidences supporting the idea that AM symbiosis can be used to develop agronomic practices for sustainable rice production and rice resistance to abiotic stresses.

1. Introduction

In soil, fungi can be characterized by their nutritional strategy: most fungi are saprotroph obtaining nutrients from dead organic matter while a small group of parasitic or mutualistic fungi feed on living organisms. Although some fungi are always in one category, others can switch among the saprotrophic, parasitic and mutualistic lifestyles depending on circumstances. In natural ecosystems, mycorrhizal fungi can be found as free-living organisms but need to associate with plant roots in order to complete their life cycle. This association is categorized as mutualistic because the fungus improves plant nutrient acquisition, water absorption, growth and resistance to biotic and abiotic stresses, while the host plant provides carbohydrates nutrients to the fungus allowing its growth and development (Bonfante and Genre, 2010).

Mycorrhizal fungi emerged with plant colonization of land around 450 million years ago (Remy et al., 1994; Taylor et al., 1995). Coincidentally, the earliest association of plant with fungus was dated to 407 million years ago, suggesting that ancestral plant-fungus symbiosis may have facilitated plant transition from aquatic to continental environments (Strullu-Derrien et al., 2014). Today, mycorrhizal fungi can associate with over 90% of higher plant species (including agricultural crops) and are found in soil of all continents from alpine lands to tropical forests and from grasslands to croplands (Smith and Read, 2008).

Mycorrhizas have been divided into two major types on the basis of the anatomical aspects of their interaction with the roots of the host-plant: (1) ectomycorrhizas involving septate fungi from the Ascomycota and the Basidiomycota phyla in which fungal hyphae (long filamentous structure) surround the root tips and develop between epidermal cells but never enter the cell lumen, and (2) endomycorrhizas including ericoid, orchid and arbuscular mycorrhizas, in which the fungus penetrates and develops inside cells of plant roots (for review see Bonfante and Genre, 2010). Arbuscular mycorrhizas (AMs) are the most common and ancestral type of mycorrhizas, involving primitive aseptate fungi from Glomeromycota phylum. At the present time, arbuscular mycorrhizal fungi (AMF) have been classified into four orders (Diversisporales, Glomerales, Archaeosporales and Paraglomerales) of the

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https://doi.org/10.1016/j.rhisph.2018.08.003
Received 2 July 2018; Received in revised form 28 August 2018; Accepted 29 August 2018
Available online 30 August 2018
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Glomeromycota phylum (Redecker et al., 2013). In AM symbiosis, the fungus creates in the soil a complex network of hyphae specialized in the absorption of minerals such as inorganic phosphorus (Pi) and nitrogen (N), and develops highly branched organs called arbuscules in root cortical cells that allow bidirectional exchange of resources with the plant (for recent review see Choi et al., 2018; Smith and Smith, 2011). The beneficial effects of AMF on plant performance raises the interest of using AM symbiosis for improving crop productivity in a context where agriculture will need its "ever green" revolution to adapt to future climates.

Rice is the staple food for more than half of the world's population, providing more than 20% of the daily calories to about 3.5 billion people on the planet (Global Rice Science Partnership, 2013). The two species of cultivated rice are *Oryza sativa* (Asian rice) and *Oryza glaberrima* (African rice). *O. sativa* was domesticated approximately 10,000 years ago from wild progenitor *Oryza rufipogon* and/or *Oryza nivara* in the Yangtze Valley in China, the Ganges Valley in India and the north-east India/Bangladesh/north-west Burma giving rise to subsequent subpopulations japonica, indica and aus, respectively, through allele introgressions (Choi et al., 2017; Choi and Purugganan, 2018; Fuller et al., 2010). *O. glaberrima* was domesticated from its wild relative *Oryza barthii* around 3 000 years ago in the Inner Niger Delta (Cubry et al., 2018; Meyer et al., 2016; M. Wang et al., 2014). *O. sativa* is a high yielding crop widely cultivated across the world while *O. glaberrima* has less grain yield but is relatively more stress tolerant and its cultivation is restricted to Africa (Huang et al., 2015). Rice is mainly produced in irrigated lowland environments where fields are consistently flooded throughout the cropping season. The rest of the rice production is provided by rainfed lowland and deep-water rice cultivation where soils are temporally flooded, and rainfed upland rice cultivation where the soils are generally aerobic (Global Rice Science Partnership, 2013). In many irrigated environments, rice is grown as a monoculture with two crops a year. However, significant areas of rice are also grown in rotation with a range of other crops, including wheat or maize (Global Rice Science Partnership, 2013).

Rice consumption is continuously growing across the world and achieving food needs forecast will require an increase in rice production (Seck et al., 2012). In sub-Saharan Africa where rice is becoming a food staple, the gap between demand and supply has reached 10 million metric tons in 2008, costing the region an estimated $3.6 billion for imports and leading to development plan aiming at increasing local production (Muthayya et al., 2014). Strategies aiming at increasing rice production have to take into account climate change that is associated with increasing temperatures and less-regular and predictable rain pattern with stresses such as heat, drought or salinity having increasing impact on crop production (Atlin et al., 2017; Bin Rahman and Zhang, 2018; Johnson et al., 2018; Stott, 2016; Ummenhofer and Meehl, 2017; Varshney et al., 2018; Wheeler and von Braun, 2013). In West-Africa, where rice is mainly cultivated under non-flooded environments, a study simulating the impact of climate change on rice production has shown that the yield of rice in the wet season would decrease by − 21% without adaptation to extreme temperatures but increase by + 7% if photosynthesis is improved along with nutrient and water management (van Oort and Zwart, 2018).

To improve rice production and sustainability at lower environmental cost, i.e., by reducing water demand and greenhouse gas emission along with improving soil fertility, the use of beneficial symbiotic microbes such as AMF is emerging. One goal is to improve the beneficial impacts of rice AMF interaction by identifying genes/traits controlling symbiotic outcome that could be targeted for breeding purposes (Nakagawa and Imaizumi-Anraku, 2015; Sawers et al., 2018). Alleviation of abiotic stresses detrimental effects by AM symbiosis primarily relies on improved water and mineral nutrition in rice mycorrhized plants that can further improve physiological traits such as root hydraulic conductivity or photosynthesis efficiency (Aroca et al., 2012; Dodd and Ruiz-Lozano, 2012; Porcel et al., 2015; Rodriguez and Redman, 2008; Ruiz-Sánchez et al., 2011; Schützendübel and Polle, 2002; Zhang et al., 2005). In field, AM symbiosis establishment and plant responsiveness after inoculation are particularly dependent on environmental conditions that often make the identification of specific AMF beneficial effects difficult (reveiwed in Igiehon and Babalola, 2017; Köhl et al., 2016). In this review, we will give an overview of the molecular mechanisms involved in the establishment of AM symbiosis in plants, with particular focus on recent discoveries in rice. Furthermore, we will provide arguments showing that AM symbiosis is not marginal in rice agrosystems and could be exploited to improve rice resistance to abiotic stresses, which requires the selection of suitable combination of cultivar, fungus and agricultural practices.

2. Am symbiosis establishment

In the past decade, significant progress was made in the understanding of the signals used by AMF and the host plant to recognize each other as well as the cascade of molecular event allowing AM symbiosis establishment and its maintenance (for recent review see Bucher et al., 2014; Nakagawa and Imaizumi-Anraku, 2015; Kamel et al., 2017; Luginbuehl and Oldroyd, 2017; Choi et al., 2018). A number of genes involved in pre-infection signaling, root infection and arbuscule development have been characterized mainly in leguminous plants such as *Medicago truncatula and Lotus japonica* that are able to establish AM symbiosis as well as root nodule symbiosis through an early common signaling pathway. Rice, that is mainly cultivated in waterlogged conditions that are presumably less favorable for AMF survival and root infection, received relatively less attention due to low stakes of AM symbiosis in such environments. Climate change and increased water scarcity has recently resulted in recasting rice cultivation towards non-flooded environments renewing the interest of using rice as a model plant for studying AM symbiosis (Nakagawa and Imaizumi-Anraku, 2015). In the following section, we will describe AM symbiosis establishment in rice in the light of the knowledge obtained in other species such as *M. truncatula*, *L. japonica* and *Arabidopsis thaliana*.

2.1. Pre-infection signaling events

The pre-symbiotic dialogue between AMF spores located at the vicinity of plant roots involve chitin-derived signaling molecules (Myc-factors) secreted by the AMF spores and plant derived molecules such as strigolactones (SLs) and cutin monomers (Bonfante and Genre, 2015; Genre et al., 2013; Maillet et al., 2011). SLs are components of root exudates and are known to promote AMF hyphal branching that is a prerequisite in AM symbiosis (Akiyama et al., 2005). SLs are carotenoid-derived phytohormones that were first characterized as seed germination stimulants for root parasitic weeds belonging to the genus *Striga* (Cook et al., 1966). In rice, as in other plants, SLs biosynthesis starts by the isomerization of β-carotene by a β-carotene isomerase DWARF27 (D27). The product of this isomerisation is cleaved by two carotenoid cleavage dioxygenases DWARF10 (D10) and DWARF17 (D17) resulting in the formation of carlactone (Alder et al., 2012; Seto et al., 2014). Carlactone is further converted into 2'-epi-5-deoxystrigol after oxidation by rice *Os*900, homologous to the Arabidopsis MORE AXILLARY GROWTH1 (MAX1) that belongs to the family of cytochrome P450 (Cardoso et al., 2014b; Zhang et al., 2014). SLs are likely mainly produced in the root cortex, and can be transported from the root to the soil to promote AMF infection, but also from the root to the shoot to control branching (for review see Saeed et al., 2017). In petunia and Arabidopsis, a PDR-type ATP-binding cassette transporter that remains uncharacterized in rice facilitates the release of SLs in the rhizosphere via hypodermal cells (Borghi et al., 2016; Kretzschmar et al., 2012; Sasse et al., 2015). Mutation in rice *DWARF14 (D14)* encoding α/β-fold hydrolase leading to SL insensitivity and increased SLs synthesis induced higher root infection by AMF as compared to the wild type plants (Gutjahr et al., 2015; Umehara et al., 2008; Yoshida et al., 2012).

Interestingly, mutation in *DWARF14* paralog *DWARF14LIKE* (*D14L*) lead to an absence of hyphal physical contact and characteristic transcriptional responses to fungal signals (Gutjahr et al., 2015). The *d14l* mutant plant still responds to SLs but is insensitive to karrikin, a butenolide compound derived from wild-fire smoke that shares molecular characteristics (butenolide moiety) with SLs and uses similar signaling pathways (De Cuyper et al., 2017; Flematti et al., 2004). This indicates that rice D14L is involved in the detection of this non-plant derived compound by possibly creating permissive condition for AM symbiosis by a mechanism that is yet to be discovered (Gutjahr et al., 2015).

Cutin is also considered as root exudates promoting AM symbiosis (Bonfante and Genre, 2015). Cutin is composed of cutin monomer, typically from the C16:0 and C18:0 lipid families, and is known to constitute an outer hydrophobic layer at the cell surface of aerial tissues preventing excessive water loss (Pollard et al., 2008). In roots, it was demonstrated that cutin is a signaling molecule involved in AM symbiosis establishment. Indeed, application of exogenous lipid monomers can complement the absence of AMF infection in the *M. truncatula ram2* mutant that is deficient in cutin monomers production (Wang et al., 2012). Although, the precise role of cutin exudation in this early stage of the symbiotic interaction remains unclear, it may well represent substrates for AMF cutinase and contribute to fuel hyphal growth (Keymer et al., 2017; Murray et al., 2013).

Plant-derived SLs and cutin can be perceived by the AMF and induce production of fungal chitin-derived signaling molecules (Myc-factors; Fig. 1A). In rice, the CHITIN ELICITOR RECEPTOR KINASE1 (*Os*CERK1) protein, a Lysin-motif receptor-like kinase homologous to the Nod factor receptors NFR1 and NFR5 of *L. japonica* and LYK3 and NFP of *M. truncatula*, was identified as a potential receptor for fungal chitooligosaccharide signals and is necessary for the establishment of AM symbiosis (Amor et al., 2003; Limpens et al., 2003; Madsen et al., 2003; Radutoiu et al., 2003; Zhang et al., 2015).

As the fungal hyphae grows and approaches the root in response to SLs and cutin, the secreted Myc-factors trigger calcium oscillations in root epidermal cells and a signal transduction cascade that is mediated by components of the so-called common symbiosis signaling pathway that also governs rhizobial infection during nodulation in legumes (Oldroyd, 2013). These components are conserved in rice. *OsSYMRK* encodes a LRR protein kinase involved in symbiotic signal perception. Downstream, *OsCASTOR* and *OsPOLLUX* encoding two potassium channels located in the nuclear membrane act as activator of Ca^{2+} spiking, *OsCCaMK/OsDMI3* encoding a Ca^{2+}/Calmodulin-dependant protein kinase acts as decoders of the Ca^{2+} signals, and *OsCYCLOPS/OsIPD3* encoding a transcription factor acts as transducer of the Ca^{2+}-signals (Chen et al., 2009, 2008, 2007; Gutjahr et al., 2008). Interestingly, the existence of an alternative AM-signaling pathway that is independent of the common symbiosis signaling pathway has been suggested in rice, but its molecular determinants remain unknown (Gutjahr et al., 2008).

2.2. Root infection

The first infection event consists in the formation of an hyphopodium, a specialized AMF hyphae, often branched and swollen, which flatten on the cell wall surface of few root epidermal cells before intracellular fungal penetration (Fig. 1B; Bonfante and Genre, 2010). Lateral roots are primary sites of hyphopodium formation where they tightly adhere to epidermal cells by forming protubules with many digitations into the outer layer of the plant cell wall (Genre et al., 2005). It has been demonstrated in *M. truncatula* that hyphopodium development is followed by a pause in fungal growth that can last for 4–6 h where epidermal cells reorganize their cytoplasm for hyphal penetration (Genre et al., 2005). The nucleus of the cortical cell in contact with the infected rhizodermis cell migrates and positions itself underneath the hyphopodium to finally traverse the plant cell vacuole and initiate the formation of a prepenetration apparatus (Fig. 1B; Genre et al., 2009). Prepenetration apparatus is a subcellular structure resembling to a tube that the cell in contact of the hyphopodium will form to accommodate intracellular hyphal growth (Genre et al., 2008).

Downstream of the common symbiosis signaling pathway, AM-associated responses and hyphopodium formation are mediated by REDUCED ARBUSCULAR MYCORRHIZA1 (RAM1, named *Os*GRAS2 or *Os*RAM1 in rice), a GRAS-domain transcription factor that represents the diversion point from nodule symbiosis pathway (Gobbato et al., 2012; Yu et al., 2014). RAM1 has been particularly studied in *M. truncatula* and *L. japonicus* where *ram1* plants are deficient in AM infection due to defect in differentiation of tip-growing hyphae into a hyphopodium upon contact with the root (Gobbato et al., 2012; Pimprikar et al., 2016). In *L. japonicus*, *RAM1* is activated by direct binding of a CYCLOPS/CCaMK complex to a *cis* element of its promoter (Pimprikar et al., 2016). It has been demonstrated in *M. truncatula* that RAM1 regulates the expression of *REDUCED ARBUSCULAR MYCORRHIZA2* (*RAM2*) that encodes a glycerol-3-phosphate acyl transferase involved in the production of cutin monomers (Gobbato et al., 2012; Wang et al., 2012). Mutation in *RAM2* induced similar phenotype than in *RAM1* that can be reversed by application of C16 aliphatic fatty acids, suggesting that cutin monomers, besides promoting hyphal growth, may contribute to hyphopodium formation (Keymer et al., 2017; Wang et al., 2012). In *L. japonicus*, prepenetration apparatus formation requires CCamK kinase activity in the nucleus (Takeda et al., 2012), as well as the phosphorylation of its target CYCLOPS (Singh et al., 2014; Yano et al., 2008). It remains to be determined if CCamK and CYCLOPS rice homologs have the same function in prepenetration apparatus formation.

SLs are also involved in hyphopodium formation and control of AM infection. In rice, mutation of *D10* and *D17* genes involved in SL-biosynthesis induced severe reduction in hyphopodium formation and intraradial infection (Gutjahr et al., 2012; Kobae et al., 2018). Interestingly, mutation in rice *DWARF3* (*D3*) encoding a F-box Leu-rich repeat protein involved in SLs receptor complex that also resulted in increased SLs synthesis induced arrested hyphopodia development by a mechanism that remains unknown (Umehara et al., 2008; Yoshida et al., 2012).

In addition to SLs and cutin, N-acetylglucosamine (GlcNAc) is another plant factor that was recently shown to be required for hyphopodium formation and AM symbiosis (Nadal et al., 2017). Mutation in rice *NO PERCEPTION1* (*OsNOPE1*) that encodes an GlcNAc transporter from the Major Facilitator Superfamily induced aberrant hyphopodium formation. Rice *Os*NOPE1 mediates GlcNac transport *in planta* and the absence of AM symbiosis in *nope1* can be restored in presence of wild-type root exudates, suggesting that GlcNAc exudation mediated by *Os*NOPE1 is a necessary process for hyphopodium establishment (Nadal et al., 2017).

2.3. Arbuscule development and function

Formation of intercellular tree-shaped hyphal branching during arbuscule development involves intensive restructuring of cortex cells cytoskeleton (Fig. 1C; reviewed in Gutjahr and Parniske, 2013; Choi et al., 2018). Arbuscule initiation is associated with expression of marker genes with elusive function, such as subtilisin-like Ser protease (*SbtM1*) in *L. japonicus* or blue copper-binding protein1 (*BCP1*) in *M. truncatula*, and necessitates VAPYRINs involved in membrane fusion processes and protein-protein interaction (Feddermann and Reinhardt, 2011; Pumplin and Harrison, 2009; Takeda et al., 2009). Homologs of these arbuscular initiation-associated genes have not been identified yet in rice.

Development of arbuscules and fungal growth further rely on the delivery of plant sugars and fatty acids at the periarbuscular membrane (PAM) of the infected cortex cells which represents the plant border delimitating, with the fungal hyphae, the periarbuscular space. Differential regulation of genes controlling carbohydrates metabolism

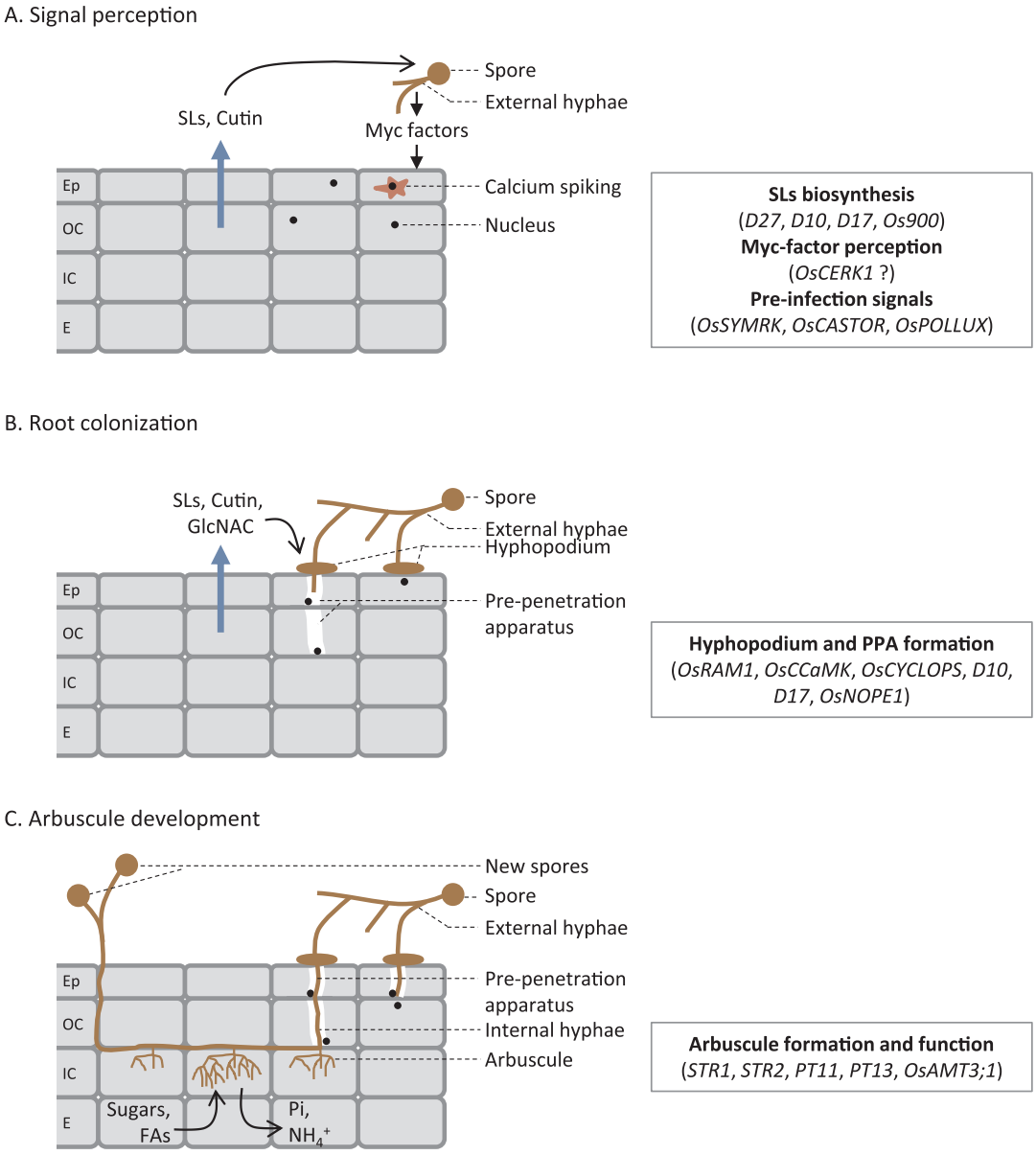

Fig. 1. Schematic view of AMF infection process and rice genes involved. (A) Strigolactones (SLs) and cutin monomers are exudated from roots and induce AMF hyphal growth. Concomitantly, Myc factors are secreted by AMF and are perceived by roots that induce genes from the common symbiosis pathway and pre-infection signals such as calcium spiking. (B) When reaching the root epidermal surface, hyphal tips develop into a hyphopodium that represent the first AM infection event mediated by *OsRAM1* in rice. N-acetylglucosamine (GlcNAc) whose transport is mediated by *Os*NOPE1 in rice, as well as SLs and cutin are required for hyphopodium formation as possible sources of carbon. In cells located directly under the hyphopodium, intense cytoplasm reorganization result in the formation of a pre-penetration apparatus that guides hyphal penetration through the inner cortex where arbuscules are initiated. (C) Arbuscule development relies on the delivery of plant sugars and fatty acids at the periarbuscular membrane that are translocated from the plant to the AMF through STR1 and STR2 in rice. In exchange, AMF transfer inorganic phosphate and ammonium to the rice plant through PT11 and *Os*AMT3;1, respectively. Arbuscule development is controlled by plant carbon, phosphorus and nitrogen status and has a lifetime of two to three days. Ep: epidermis; OC: outer cortex; IC: inner cortex; E: endodermis; SLs: strigolactones; PPA: pre-penetration apparatus; FAs: fatty acids; Pi: inorganic phosphate; NH_4^+: ammonium.

and sucrose transporters occurs upon root infection in order to redirect sugars towards the infected cortex cells (Manck-Götzenberger and Requena, 2016; for recent see Roth and Paszkowski, 2017). In rice, comparative expression analyses of roots infected or not by AMF showed a clear induction of plant sugar transporter *Os*SWEET3b in mycorrhized roots (Fiorilli et al., 2015). At the PAM, sugars mainly in the form of hexose can be directly transported to the periarbuscular space by uncharacterized sugar transporters to be further transferred into the arbuscule by fungal Monosaccharide Transporter2 (MST2; Helber et al., 2011). In infected cortex cells, sugar can also be transformed into fatty acids by *FAS* encoding a fatty acyl synthase, *FatM* encoding an acyl-carrier protein-thioesterase and RAM2, and transferred to the fungus to promote arbuscular development. Indeed, mutation in *M. truncatula FatM* and *RAM2* induce severe reduction in arbuscular growth (Bravo et al., 2017; Wang et al., 2012). Recently, the identification of a novel AM-specific β-*keto-acyl ACP synthase I* (*KASI*) gene in *L. japonicus*, combined with lipidomics and isotope profiling of fatty acids, lead to a model, where AM-infected cells express AM-specific lipid biosynthesis genes (*KASI*, *FatM*, *RAM2*) to specifically synthetize high amount of 16:0 fatty acids and 16:0:β-monoacylglycerol from sugars (Keymer et al., 2017). Two half-size ABC transporters STR1 and STR2 of the PAM, originally identified in rice, are further involved

in the diffusion of fatty acids to the fungus (Bravo et al., 2017; Gutjahr et al., 2012). Therefore, it is proposed that KASI, FatM, RAM2, STR1 and STR2 form an AM-specific operational unit for plant lipid biosynthesis and transfer to the arbuscules (Bravo et al., 2017; Keymer et al., 2017).

As a symbiotic interaction, AMF exchange nutrients to the plant against carbohydrates (Fig. 1C). AMF contribution to plant P uptake is considered as a key physiological process by which AMF improve plant growth (Smith and Smith, 2011). Two rice PHOSPHATE TRANSPORTER, PT11 and PT13, belonging to the $Pi:H^+$ symporters family and located in the PAM have been shown to be important for arbuscular development. Indeed, *pt11* and *pt13* mutants showed drastic reduction in arbuscule formation and the ones that formed showed reduction of their surface (Guimil et al., 2005; Paszkowski et al., 2002; Poirier and Bucher, 2002; Yang et al., 2012). PT11, the rice ortholog of *M. truncatula* PT4, is the only monocot AM-specific Pi transporter localized in the PAM delivering Pi from the arbuscules to the cortical cells (Javot et al., 2007; Kobae and Hata, 2010; Paszkowski et al., 2002; Yang et al., 2012). Indeed, PT13 has no transport activities and may be involved in the sensing of Pi (Yang et al., 2012). In addition to Pi, AMF can improve plant nutrition towards nitrogen. Ammonium (NH_4^+) transporters from the AMT2 family were found to be required for arbuscular maintenance through signaling functions in *M. truncatula* while AMT3 are suggested to be involved in ammonium transfer from AMF to rice plants (Breuillin-Sessoms et al., 2015; Koegel et al., 2017; Pérez-Tienda et al., 2014).

Sugar, Pi and N signaling may represent ways for the plant to control arbuscular development, where P and N starvation induce arbuscule maintenance while limitation of carbon supply to the fungus is associated with arbuscule collapse (Choi et al., 2018; Javot et al., 2011; Roth and Paszkowski, 2017; Yang et al., 2012). Hormones also fit into the scenario of AM symbiosis establishment and arbuscular development. SLs, auxin and abscisic acid generally act as positive regulators while gibberellin, ethylene and salicylic acid act as repressor of arbuscular development, when the role of brassinosteroid, cytokinin and jasmonic acid still remains unclear (reviewed in Foo et al., 2014). For instance, application of gibberellic acid to rice plants as well as mutation in *SLENDER* (*SLR*) encoding the unique rice DELLA protein (a repressor of gibberellic acid signaling) both severely impaired AM infection (Yu et al., 2014). In *M. truncatula*, DELLA proteins are required for arbuscule formation and contribute to the induction of *RAM1* upon AM-perception by physical interaction with CYCLOPS within the CCaMK-CYCLOPS complex (Floss et al., 2013; Pimprikar et al., 2016). Interestingly enough, these extremely controlled and sophisticated structures are ephemeral with a lifetime at maturity of generally two to three days, as demonstrated by live cell imaging of arbuscule development using rice lines expressing the PAM-localised *PT11prom*:PT11:GFP marker gene (Kobae and Hata, 2010).

3. Rice morphological and ecological factors controlling Amf infection

3.1. Rice root morphology, anatomy and exudation

Rice plants have a complex fasciculate root system that is comprised of different root types (for review see Rebouillat et al., 2009). The radicule first emerge from the rice seed and is followed by formation of embryonic crown roots that emerge from the coleoptilar node. Later, adventitious postembryonic crown roots emerge from the stems nodes of the different tillers. Radicule and crown roots give rise to two types of lateral roots: large lateral roots that have indeterminate downwards growth and fine lateral roots that have determinate agravitropic growth. Large lateral roots support fine lateral roots and can form more large laterals of several orders (Rebouillat et al., 2009). The radial anatomy of rice roots is typical of that found in semi-aquatic plants, with formation of extensive aerenchyma (large air filled lacunae in the cortex) and apoplastic barriers (a sclerenchyma underneath the rhizodermis and an exodermis surrounding the root stele; Clark and Harris, 1981; Rebouillat et al., 2009). Aerenchyma are extensively present in rice roots and are found in all root types excluding fine lateral roots which lack cortex tissue (Rebouillat et al., 2009).

Plant root system infection by AMF is non-random and some root types are more prone to be infected than others. It is generally admitted that AMF preferentially infects lateral roots rather than coarse roots such as crown roots in monocotyledon or primary root in dicotyledon plants (Gutjahr and Paszkowski, 2013). In rice, Gutjahr et al. (2009) showed that AM infection is preferentially observed in large lateral roots. Nevertheless, over long periods of rice co-cultivation with AM fungi, infection of portions of crown roots can be observed (Gutjahr and Paszkowski, 2013). Interestingly, strong infection was also observed in fine lateral roots although these roots seem not recognized by AMF (no hyphopodium differentiation observed) and cannot develop arbuscules due to the absence of cortex tissue. This unequal distribution of AM infection in rice may be explained by the developmental, anatomical and chemical properties of the different types of roots. Large lateral roots usually have expending tissues with cell-wall flexibility that may facilitate AMF accommodation (Gutjahr et al., 2009). Conversely, crown roots are rigid, characterized by highly lignified parietal barriers and by the presence of large aerenchyma that may be more challenging to infect (Gutjahr and Paszkowski, 2013). Non-recognition of fine lateral roots by AMF may be due to their surface or exudates composition. Interestingly, a number of SLs structural analogs with differential activities on hyphal branching can coexist and be exudated from rice roots and therefore may influence the specificity of AMF root infection (Cardoso et al., 2014a).

Rice exhibits large variability in root architectural traits that are related to the organization of the species into varietal groups and the adaptation of these groups to their cultivation systems (Lafitte et al., 2001; O'Toole and Bland, 1987). As a general trend, *indica* varieties are characterized by thin, superficial roots with narrow vessels while japonica varieties have smaller number of roots which are deeper and thicker with larger vessels (Lafitte et al., 2001). Root system architecture, which refers to the special arrangement of the whole root system in the soil, has recently been shown to greatly influence plant ability to extract nutrient and water and therefore tolerance to abiotic stresses (Rogers and Benfey, 2015). It is therefore attractive to think that, by controlling rice root system architecture and root anatomy, it may be possible to influence root system infection and extension through AMF hyphal mycelium (Gutjahr and Paszkowski, 2013; Maherali, 2014).

3.2. Rice cropping systems

Agricultural practices such as tillage, monoculture, chemical fertilization or pest control can greatly impact AMF community in agricultural lands. In the case of rice cultivation, the most limiting factor for the presence of AMF in the soil is the anaerobic irrigated cultivation that provides about 75% of the world's rice production (Global Rice Science Partnership, 2013). Since AMF are aerobes in nature, it is generally admitted that establishment of rice AM symbiosis will have the most impact in aerobic rice cultivation (van Oort and Zwart, 2018). To save water, alternate wet and dry (AWD) cultivation have been developed. AWD consists in switching from a continuously flooded rice field to a field that encompasses several dry phases during the growing season. This cultivation system reduces water use by 30% without impacting the crop yield (Bouman and Tuong, 2001; Lampayan et al., 2015). In addition, AWD reduces the emission of methane, a greenhouse effect gas, by reducing anaerobic degradation of organic matter by methanogenic bacteria and archaea (Conrad, 2007; Sander et al., 2014). Watanarojanaporn et al. (2013) analyzed the indigenous AMF community structure within flooded and AWD cultivation systems and showed that rice cultivated under AWD-managed plots had increased

diversification of AMF communities. Furthermore, rice plants cultivated under AWD showed higher percentage of root infection by AMF, P uptake and biomass as compared to plants cultivated under flooded conditions, confirming the hypothesis that mycorrhizal response index is greater under aerobic conditions (Watanarojanaporn et al., 2013). However, similar levels of rice root infection by AMF have been observed under waterlogged soil as compared to aerobic soil, but delayed in time in the former condition (Diedhiou et al., 2016; Lumini et al., 2011; Watanarojanaporn et al., 2013). It is proposed that under waterlogged soil conditions, AMF survives because it can exchange gas through rice root aerenchyma.

Establishment of symbiotic interactions between rice roots and AMF can significantly improve the plant P uptake ability by increasing the volume of scavenged soil (Solaiman and Hirata, 1997). In rice, AMF can contribute up to 80% to the rice plant P uptake (Yang et al., 2012). However, it is well-documented that high concentration of P in soil has a negative impact on AM symbiosis establishment presumably making such AM beneficial effect on P nutrition possible only when soil P content is low (reviewed in Smith and Smith, 2011). In high-input rice cropping systems, P fertilization is applied to rice fields in order to obtain optimal yield but it appears that P use efficiency, that depends on the ability of the plant to take up P from the soil and on the efficiency of its allocation within the plant, is only about 25% in rice (Dobermann and Fairhurst, 2000; Roberts and Johnston, 2015). It is proposed that improving rice P use efficiency in such conditions relies on breeding for uptake- and internal P use-related traits while AM symbiosis is poorly considered because likely inhibited (Heuer et al., 2017; van de Wiel et al., 2016). However, Kobae et al. (2016) showed that P treatment on AM infected rice roots temporally inhibited new arbuscules development but did not alter the activity and longevity of preformed arbuscules and AMF vesicles. These results open ways to better evaluate the possible role of AM symbiosis in increasing rice P use efficiency in high-inputs rice cropping systems with optimized fertilizer dose and application time.

Conversely, poor (P-fixing, aluminium rich…) and problematic soils (saline, alkaline…) represent around 40% and 75% of the total rice growing areas in Asia and Africa respectively, which correspond to poor regions of the world where inputs for agriculture are low (Gamuyao et al., 2012; Haefele et al., 2014). In these regions, P deficiency is an important limiting factor for rice growth and yield since it alters phospholipids, DNA, RNA synthesis as well as other nucleotide containing molecules that provides plant cells the energy required for metabolic and catabolic cellular processes (Heuer et al., 2017). In such soils, improving P use efficiency requires efficient high-affinity Pi uptake capacities that can be achieved by higher lateral root and root hair production, and exudation of organic acids or molecules promoting AM symbiosis establishment (Heuer et al., 2017; van de Wiel et al., 2016; Wang et al., 2017).

Rice is generally grown as a monoculture in irrigated lowland areas (Global Rice Science Partnership, 2013). However, crop rotation between flooded rice and non-flooded maize or wheat is becoming more common, particularly in South-Asia (India and Bangladesh; Timsina et al., 2010). Crop rotation between lowland rice and upland maize was shown to greatly influence the microbial communities associated with roots of both crops, with possible positive effects on AMF population (Breidenbach et al., 2017). In line with these results, Maiti et al. (2011a) showed that rice rotation with maize followed by *Macrotyloma uniflorum* in the first year and upland rice Vandana in the second year induced an increase in rice infection by AMF, P acquisition and grain yield. When crop rotation is not practiced and land is kept as fallow, off-season tillage is usually performed to control weed and soil-borne disease but have deleterious effects on the activity of native AMF (Verzeaux et al., 2017). In rainfed upland cultivation systems, agronomic recommendations to reduce land tillage has been proposed in order to minimize these detrimental effects on AMF communities and favor rice infection by AMF in the next growing season, which consist in a maximum of two off-season tillage at 13 weeks intervals (Maiti et al., 2011b).

4. Improvement of rice growth and resistance to salinity and drought stress by Am symbiosis

AM symbiosis can promote plant growth and enhance plant resistance to a variety of abiotic stresses. Increased plant fitness and protection by AM symbiosis involve direct beneficial effects of AMF on structuring the rhizosphere, enhancing water and mineral nutrition while excluding toxic ions. AM symbiosis also changes plant gene expression and phytohormone balance affecting physiological processes related to plant metabolism, growth and development. Therefore, AM symbiosis go well beyond a standard bidirectional carbon and Pi transfer, but lead to interlinks outcomes that increase plant protection against abiotic stresses. In the following sections, we focus on the AM symbiosis direct and indirect effects on rice growth and protection under nutrient deficient, salinized and water deficient soils. These stresses are among those that most restrict rice growth and production worldwide, and where AM symbiosis may arguably have prominent protection role.

4.1. Nutrient uptake for improved growth in nutrient deficient soils

It is well established that low-P conditions induce plant root infection by AMF (Smith and Smith, 2011). In rice, inoculation with AMF can improve P nutrition in controlled laboratory environment as well as field conditions under lowland or upland conditions (Maiti et al., 2011a; Paszkowski et al., 2002; Solaiman and Hirata, 1997; Yang et al., 2012). AM plants can absorb P by two distinct pathways: the direct uptake pathway through epidermis and root hairs, and the AM pathway through fungal extraradical mycelium. When absorbed at the extraradical mycelium, Pi molecules assemble to form polyP corresponding to linear chains of Pi residues linked by phosphoanhydride bonds (Fig. 2A; reviewed in Smith and Smith, 2011). PolyP chains travel along hyphae to be hydrolyzed back into Pi in arbuscules and translocated to cortical cells through rice PAM Pi transporters PT11 (Fig. 2A; Yang et al., 2012). It appears however that the contributions of the direct pathway and AM pathway are not additive (Fig. 2A). In rice plants infected by AMF, the amount of P transiting through the AM pathway is largely predominant on the direct pathway (80% against 20%, respectively; Yang et al., 2012). Expression studies in japonica, indica and aus rice plants infected by AMF showed downregulation of two genes encoding Pi transporters genes, *PT2* and *PT6*, contributing to the direct pathway and induction of the AM-specific Pi transporter gene *PT11* as compared to non-AM plants (Jeong et al., 2015; Paszkowski et al., 2002; Yang et al., 2012). The mechanisms involved in downregulation of the direct pathway in AM plants remain elusive but may be explained by the better overall P status of the plant (Gu et al., 2016; Młodzińska and Zboińska, 2016). However, downregulation of the direct pathway has been observed independently of the P status in barley, suggesting that unknown AM-specific signals controlling expression of Pi transporters may exist (Glassop et al., 2005).

In addition to Pi, AMF can efficiently transfer nitrogen (N) to the rice plant, improving its N nutrition (Courty et al., 2015; Koegel et al., 2017; Pérez-Tienda et al., 2014). AMF can use inorganic forms of N as NH_4^+ or nitrate, and organic form of N as amino-acids (Fig. 2A; Govindarajulu et al., 2005; Leigh et al., 2009). However, NH_4^+ is likely the predominant form of N absorption because it can be assimilated directly into the glutamine synthetase/glutamate synthase cycle for its conversion into arginine (Courty et al., 2015; Tanaka and Yano, 2005). Current models propose that arginine positively charged is transported along with PolyP that is negatively charged until the arbuscules in order to keep ionic charge balance. In the arbuscules, arginine is converted back to NH_4^+ to be transferred to the periarbuscular space then to the plant via plant ammonium transporter (AMT; Courty et al., 2015). The

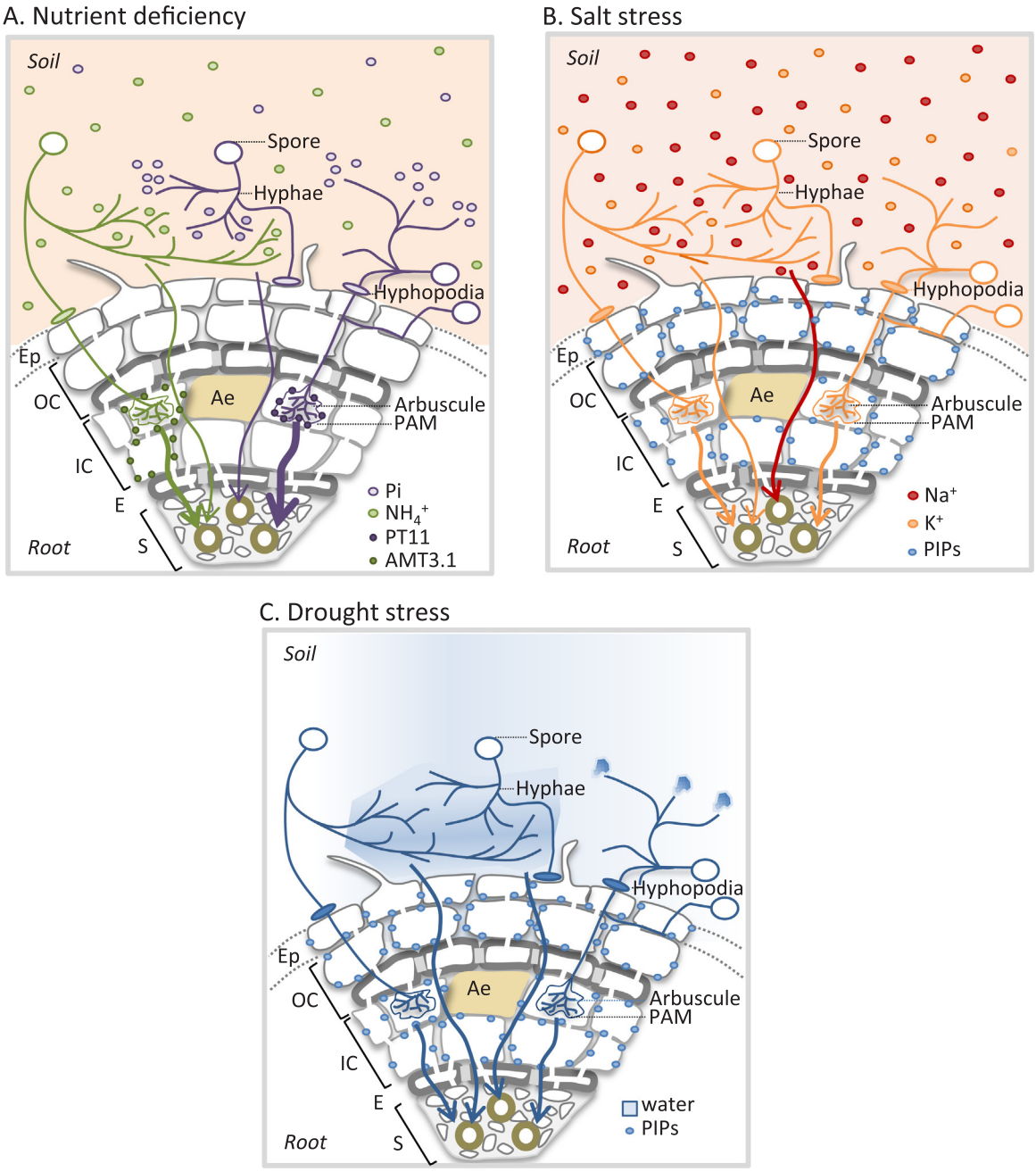

Fig. 2. Schematic view of the possible mechanisms by which AM symbiosis directly contributes to improve plant resistance to nutrient deficiency, salt and drought stress. (A) Under nutrient deficiency conditions, phosphate and ammonium scavenged by fungal hyphae are absorbed and translocated to the arbuscules before being transferred to the plant. PT11 located at the periarbuscular membrane contributes to phosphate transfer to rice roots infected by AMF while *Os*AMT3;1 is possibly involved in the redistribution of the ammonium uptake from the AM pathway. In rice roots infected by AMF, down-regulation of transporter genes involved in the phosphorus and ammonium uptake by the plant induces a reduction of the direct uptake pathway to the benefits of the AM uptake pathway. Purple and green arrows represent phosphorus and ammonium fluxes respectively. (B) In saline soils, it is suggested that AMF contributes to ionic balance by selectively taking up and transferring potassium rather than sodium to the host plant resulting in higher potassium:sodium ratio and increased resistance to salt stress. Root infection by AMF is also associated with an increase expression of specific aquaporins under salt stress that contributes to root osmotic adjustments. Red and orange arrows represent sodium and potassium fluxes respectively. (C) Under drought stress, development of dense AMF hyphal mycelium stabilizes soil structures and maintain water filled pores where plant roots and hyphal AMF can access water. AMF can also directly contribute to water uptake by scavenging water in narrow and tortuous pores. As for salt stress, increase in aquaporin expression in root infected by AMF contributes to maintain root hydraulic properties under drought. Blue arrows represent water fluxes. Ep: epidermis; OC: outer cortex; IC: inner cortex; E: endodermis; S: stele; Ae: aerenchyma; PAM: periarbuscular membrane; Pi: inorganic phosphate; NH_4^+: ammonium; Na^+: sodium; K^+: potassium; Ca^{2+}: calcium; PIPs: aquaporins from the plasma membrane intrinsic proteins family.

PAM contains ammonium transporter that are induced during AM root infection. In rice, *OsAMT3;1* was shown to be strongly induced in roots infected by AMF as opposed to *OsAMT1;1* and *OsAMT1;3* that are down-regulated (Fig. 2A; Pérez-Tienda et al., 2014). It is suggested that, as for Pi transporters involved in the direct pathway, down-regulation of *OsAMT1.1* and *OsAMT1;3* in AM plants is linked to improved N nutrition trough the AM uptake pathway (Pérez-Tienda et al., 2014). As opposed to P, N is highly mobile in the rhizosphere making AMF scavenging for N at distance of roots not as advantageous as for P. Nevertheless, studies have suggested that AM pathway can contribute

to N supply in *Zea mays* (maize) or *Daucus carota* (Frey and Schüepp, 1993; Govindarajulu et al., 2005) and can reach up to 42% in *Lycopersicon esculentum* (Mäder et al., 2000). Furthermore, mutation in *OsAMT3;1* induced reduction in N and P uptake from the AM pathway and abolished AMF-induced growth stimulation, indicating that AM NH_4^+ transfer to the plant via *Os*AMT3;1 can significantly contribute to the beneficial mycorrhizal effects on plant nutrition (Koegel et al., 2017). In addition to P and N, root infection by AMF is also able to reduce plant starvation to sulfur (Allen and Shachar-Hill, 2009; Sieh et al., 2013), but the physiological mechanisms involved remain unclear. These nutrient transfers to the host plant require energization of the PAM that is made possible by establishment of plasma membrane potential through proton pumping by the rice H^+-ATPase *Os*HA1 (E. Wang et al., 2014).

4.2. Ionic balance and water status for improved growth in saline soils

One of the characteristics of plant subjected to saline soil is an increase in sodium (Na^+) accompanied by accumulation and impairment of potassium (K^+) nutrition. K^+ is one of the essential element that play key roles has co-factor for many enzymes important for plant metabolism (Wang and Wu, 2013). In contrast, Na^+, which compete for the same binding sites as K^+, is not essential for the plant and is rather known to affect enzymes and macromolecules structure making accumulation of this ion highly toxic for the plant (Flowers et al., 2015). Under saline soil conditions, accumulation of Na^+ in plant tissues results in low K^+:Na^+ ratio and disruption of many essential metabolic pathways that are accompanied by reduction in photosynthesis and oxidative and osmotic stresses (Flowers et al., 2015). Hence, decrease in Na^+ uptake and increase of its sequestration are major determinants of plant resistance to salt stress (Ismail and Horie, 2017).

Although AMF spore germination and hyphal growth can be affected by salt, some AMF can survive in saline soil and have been found to infect roots of halophytic plants (reviewed in Evelin et al., 2009). In fact, reduced Na^+ content and increased K^+ content under saline conditions have been observed in non-halophytic plants infected by AMF as compared to non-infected plants (Giri et al., 2007; Sharifi et al., 2007; Talaat and Shawky, 2011; Zuccarini and Okurowska, 2008). It is proposed that Na^+ reduction in AM plants under saline conditions is linked to AMF ability to selectively take up and translocate K^+ to the host plant while avoiding Na^+ uptake, resulting in an AMF buffering effect that is yet to be precisely characterized (Fig. 2B; Evelin et al., 2009; Hammer et al., 2011). In rice, while AM plants showed improved resistance to salt stress, root and shoot K^+:Na^+ ratios were similar in AM and non-AM plants, indicating that other physiological mechanisms were possibly responsible for AM protection (Porcel et al., 2016, 2015). Expression analyses of Na^+ transporters suggested that AM symbiosis limited toxic Na^+ effects in shoots by favoring Na^+ sequestration in the vacuoles of root cells in rice (Porcel et al., 2016). This reduction in shoots Na^+ content was associated with improved photosynthetic and rubisco activities as well as higher plant biomass in AM plants as compared to non-AM plants (Porcel et al., 2015).

Further indirect physiological mechanisms responsible for increased plant protection to salt stress after root infection by AMF involve osmotic adjustment. Indeed, saline soils have more negative water potential to which root cells have to adjust in order to maintain favorable gradients for water uptake and to avoid water loss (Maurel et al., 2015). Several studies have demonstrated that AM plants were able to better osmotically adjust to high Na^+ by accumulating osmoprotectants such as prolines, betaines and sugars as compared to non-AM plants (Santander et al., 2017 and references therein). However, these investigations remain somewhat contradictory depending on the different AMF-host plant combinations used and did not include rice. AM symbiosis may also play a role in alleviating salt stress by enhancing activities of antioxidant enzymes or accumulation of antioxydant compounds but no evidences of such mechanisms have been demonstrated in rice to date (Ruiz-Lozano et al., 2012 and references therein). Similarly, AM symbiosis may contribute to maintain root hydraulic properties under salt stress by modulating the expression of specific aquaporin from the plasma membrane as observed in *Phaseolus vulgaris* (Fig. 2B; Aroca et al., 2007).

4.3. Water uptake for improved resistance to drought

The soil-root-shoot hydraulic potential continuum is responsible for ascendant plant water fluxes. Reduction in soil water potential due to water deficit causes disequilibrium in this continuum and induction of compensation mechanisms by stomatal closure that typically decrease root water uptake (Tardieu et al., 2017). Resulting tissue dehydration interferes with normal plant growth and development through alterations of nutrient absorption, photosynthesis and general metabolism (Tardieu et al., 2011). In addition, combination of soil drying and root shrinking due to decreased tissue turgor create air gaps between the root and the soil matrix accentuating water potential drop at the vicinity of the root (Faiz and Weatherley, 1982). Hence, maintaining water continuity and increasing root water uptake are viewed as strategies by which plants cope with soil water deficit.

Reports have shown an increased water uptake of AM *Lactuca sativa* plants under drought stress as compared to non-AM plants (Marulanda et al., 2003; Ruiz-Lozano et al., 1995). The mechanisms by which AM symbiosis can increase plant water uptake remain elusive but several clues may shed light on this process. Firstly, development of hyphal mycelium upon AM symbiosis is known to stabilize soil structures by enmeshing soil particles and stabilizing aggregates (Hallett et al., 2009; Miller and Jastrow, 2000). Stable soil structure is further important for soil porosity and maintenance of water-filled pores where plant roots and hyphal AMF can access water (Oades, 1984). Secondly, AMF hyphae binds roots to the soil, which has been suggested to increase water retention and limit hydraulic continuity loss and thereby formation of air gap when the soil is drying (Fig. 2C; Augé et al., 2001). Finally, direct contribution of AMF to plant water uptake by water transfer from fungus hyphae to cortical cells have also been suggested (Fig. 2C). Fungal hyphae are narrower than roots with an average diameter that range from 2 to 20 μm (reviewed in Smith et al., 2010). Therefore, AM hyphae have the ability to access water in narrow and tortuous soil pores as compared to roots that can be advantageous for the water scavenging in dry soils. By using a split plant-hyphal chamber in which plant and AMF where grown in separate compartment, each containing water content sensors and separated by nylon-nets and air gap that allowed only AMF hyphae to pass, Ruth et al. (2011) estimated that the hyphal contribution to total water uptake can reach 20% in barley.

Although the effects of AMF on soil structure and conductivity of the rhizosphere soil as well as direct hyphal contribution are difficult to quantify and has to be viewed cautiously because of inconsistent reporting, it may play important role in increasing root water uptake of AM plants in some circumstances (Khalvati et al., 2005; Santander et al., 2017; Smith et al., 2010). In the context of AWD for instance, such contribution may be significant to maintain water uptake during the dry cycles allowing their extension for increased water saving. Furthermore, lowland rice cropping systems are characterized by soils with high levels of clay that tend to crack on the surface when drying and by hardpans at depth which impede root penetration but retain soil moisture (Cairns et al., 2011). In such soils, hyphal mycelium may be particularly helpful to maintain soil structure and soil root contact in surface and water scavenging in hardpans.

It has been demonstrated in rice that AM symbiosis increased root branching through production of large lateral roots by mechanisms that hypothetically involved AMF signaling molecules or changes in plant nutrient status (Gutjahr and Paszkowski, 2013; Vallino et al., 2014). This AMF-associated root system architecture response may be particularly benefiting for rice adaptation to drought stress. Indeed, lateral root were proposed to be predominant sites of water absorption in

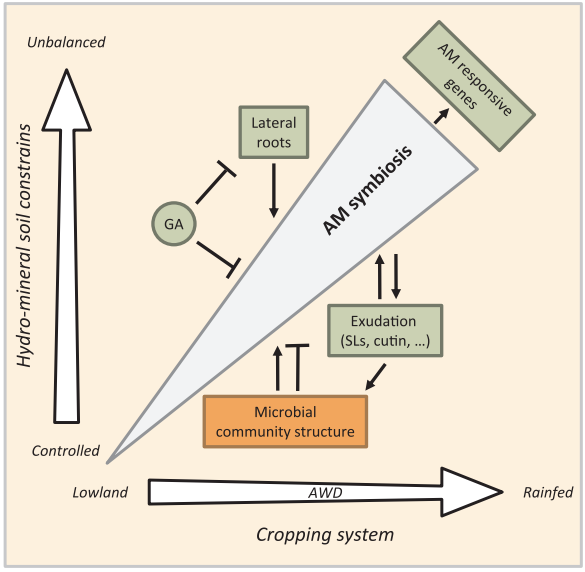

Fig. 3. Schematic diagram of breeding targets that can be considered to improve AM symbiosis in rice. AM symbiosis exists under controlled water-logged rice ecosystems, but its frequency and intensity is increased under rainfed ecosystems where soils are often unbalanced in hydro-mineral terms. Root exudation and formation of large lateral roots are under strong genetic controls in rice and represent potential targets in order to increase occurrences of AM symbiosis. Root exudation is affected by AMF root infection and modify rhizospheric microbial community structure. Therefore, AMF symbiosis indirectly influences microbes in the rhizosphere which can in return interact positively or negatively on the efficiency of the AM symbiosis, requiring the selection of right combination of plant host and AMF to improve beneficial effects. Furthermore, gibberellic acid is involved in plant growth and phenological traits but inhibits AM symbiosis. Components of the gibberellic acid signaling pathway such as DELLAs could be used to engineer plant with high AMF infection abilities and desirable architectural traits. Furthermore, genomic regions underlying AM responsive genes responsible for beneficial AMF effects represent interesting breeding targets but remain largely unknown. SLs: strigolactones; GA: gibberellic acid; AM: arbuscular mycorrhizal; AWD: alternate wet and dry cultivation.

maize (Ahmed et al., 2018) and their proliferation in rice plants cultivated in field have been associated with improved drought resistance (Henry et al., 2012). In line with these observations, AM infection significantly improves rice growth under drought conditions (Ruiz-Sánchez et al., 2011, 2010). Rice AM plants consistently showed higher stomatal conductance and photosynthesis efficiency leading to increased shoot and root biomass as compared to their non-AM counterparts. Furthermore, AM symbiosis in rice induced accumulation of osmoprotectant and antioxidant molecules while reducing accumulation of hydrogen peroxide and oxidative damage on lipids (Ruiz-Sánchez et al., 2011, 2010). Inoculation with AMF also increased water use efficiency and maintain root hydraulic conductivity through increase aquaporin expression under drought in several plant species that did not include rice (Fig. 2C; Aroca et al., 2007; Augé et al., 2001; Bárzana et al., 2014; Querejeta et al., 2006).

5. AMF: opportunities and challenges for rice breeding

Beneficial mycorrhizal effects on rice growth and resistance to abiotic stresses have often been observed in laboratory. Whether or not these effects can be repeated in much less controlled conditions, i.e., in field, and exploited by scientists to improve crop productivity remain unclear. Several reports have demonstrated that rice inoculation with AMF can improve plant growth and yield in field conditions (Diedhiou et al., 2016; Maiti et al., 2011a, 2011b; Watanarojanaporn et al., 2013). However, it remained difficult to assess the direct impact of AMF in such inoculation response because of the absence of control on the native AM community. Rice mutant unable to establish AM symbiosis could represent interesting material to estimate performance baseline and AM contribution (Gutjahr et al., 2015, 2008; Sawers et al., 2018). Regardless, such achievements will require identification of determinants controlling the efficiency of AM symbiosis in order to strengthen the consistency of beneficial mycorrhizal effects. The following sections propose clues for consideration of AM symbiosis in pre-breeding or breeding programs aiming at improving rice productivity and resistance to abiotic stresses.

5.1. Finding the right rice host-AMF combination for the right environment

AM symbiosis can promote growth and resistance to abiotic stresses in plants. However, the magnitude of beneficial mycorrhizal effects can vary depending on the plant-host combination and the environmental conditions (Smith and Smith, 2011). In addition, it is important to keep in mind that AM symbiosis can also result in plant growth depression in some cases (Santander et al., 2017; Smith et al., 2009, 2010). Absence of plant response or growth depression upon AM symbiosis may be simply explained by an imbalance between net costs and benefits, due to high plant carbon drain because of high fungal root infection or low Pi uptake because of low soil hyphal development (Li et al., 2008; Smith et al., 2010). In fact, growth depressions are not necessarily linked to the level of fungal root infection or Pi uptake efficiency but is rather associated with the specificity of the plant-AMF interaction and how the AM symbiosis affect the rhizosphere and the plant physiological response (Grace et al., 2009; Li et al., 2008).

On one hand, functional differences between AMF will influence plant response. Studies of different AMF secretomes revealed that the secreted proteins are mostly lineage specific and may therefore functionally influence host specificity and plant transcriptional reprogramming (Bucher et al., 2014; Kamel et al., 2017). Indeed, clear differences have been reported between AMF communities in different habitats and between AMF infecting different host species in the same habitat (Powell and Rillig, 2018). These observations suggest that some AMF may be more adapted to rice ecosystems and infect different varieties with varying efficiencies. Furthermore, AMF cause changes in root exudates that selectively affect communities of microorganisms in the rhizosphere, suggesting that they may play important role in the rhizosphere microbial community structure and constitute tools to better understand microbial network in rice ecosystems (Fig. 3; Marschner and Timonen, 2005; Qin et al., 2016; Rodríguez-Caballero et al., 2017; Toju et al., 2018).

On the other hand, microbial communities in the rhizosphere can be influenced by rice genotypes. A recent study of the root microbiome (Bacteria and Archaea only) of six rice cultivars, including four *O. sativa* (two japonica and two indica) and two *O. glaberrima* grown in different types of Californian soils demonstrated significant genotypic effect on associated microbial communities in the rhizosphere (Edwards et al., 2015). In total, 125 operational taxonomic units were affected by plant genotype, with the *O. glaberrima* cultivars exhibiting higher diversity in comparison with the japonica cultivars although this diversity was also influenced by the soil type (Edwards et al., 2015). Following the same types of approach, Santos-Medellín et al. (2017) recently studied the bacterial and fungal microbiome of two *O. sativa* and two *O. glaberrima* cultivars and its variation after a drought treatment in different types of Californian soils. In this study, fungal communities in the rhizosphere were significantly affected by cultivar and restructured by drought, but no genotype-drought treatment interaction were identified suggesting that the communities assembled in each cultivar responded consistently to the drought treatment. However, the large fraction of unclassified fungal operational taxonomic units in these studies limited the identification of subtle differences in genotype-treatment interaction on the fungal microbiome (Santos-Medellín et al., 2017).

When aiming at improving rice adaptation capacities through use

AM symbiosis, it will be important to define, within a particular ecosystem, the right combination of plant host and AMF. In this regard, it appears important to expend fungal taxonomic databases in order to better survey AMF communities infecting rice varieties adapted to specific rice ecosystem.

5.2. What to breed for?

SLs exudation constitutes a trait that influences AMF recruitment and establishment of AM symbiosis. Therefore, SLs exudates may be potential targets to breed for in order to favor root infection by AMF (Fig. 3). Interestingly, a number of SLs structural analogs can coexist and be exudated from rice roots (Akiyama et al., 2010). Furthermore, depending on their molecular structures, SLs analogs selectively contribute to the stimulation of AMF hyphal branching or germination of *S. hermonthica* (Akiyama et al., 2010; Cardoso et al., 2014a). Further evidences of SLs specificity come from maize where differences of SL composition in root exudates were associated with susceptibility to *S. hermonthica* but did not impact compatibility to AM fungi (Yoneyama et al., 2015). In rice, studies of SLs biosynthesis natural variation resulted in the discovery of *MAX1* and have showed that low *S. hermonthica* infection rates correlates with reduced SLs exudation in a rice Bala × Azucena population and in NERICA cultivars (Cardoso et al., 2014b; Jamil et al., 2011). These studies open ways to select rice cultivars exudating SLs promoting AMF hyphal branching but no germination of *S. hermonthica* or attraction of pathogenic microbes (López-Ráez et al., 2016).

Rice root system architecture and more precisely production of large lateral roots may represent another beneficial trait for AM root infection (Fig. 3). Therefore, engineering rice root system architecture to increase large lateral roots number may be particularly relevant to favor AM infection. A number of QTLs and genes associated with root traits such as branching or lateral root development have been identified in rice (Courtois et al., 2013; Topp et al., 2013). Large lateral roots proliferation at depth is considered as a beneficial trait for water extraction under drought stress, but maintenance of large lateral roots in top soil around AMF spores may be equally considered to maintain AM infection and efficient nutrient uptake (Lynch et al., 2014; Oehl et al., 2005). In such case, considering plant interactions with soil symbiotic microbes such as AMF when searching for root ideotypes may help to prevent trade-offs. Furthermore, number of crown roots has recently been suggested as a beneficial root trait for rice production under AWD conditions (Sandhu et al., 2017). Top-soil large lateral roots production may be added to this AWD root ideotype in order to promote root AMF infection.

Establishment and maintenance of arbuscules involve phytohormones and is accompanied by substantial transcriptional and post-transcriptional reprogramming of host roots. For instance, AM symbiosis establishment involve regulation of transcription factors from the GRAS protein family that are known to play important roles in plant development (Hirsch and Oldroyd, 2009). In particular, DELLA proteins play dual roles in promoting AM symbiosis and repressing the growth promoting hormone gibberellic acid signaling pathway (Fig. 3; Harberd et al., 2009; Yu et al., 2014). Interestingly, several cereal crop varieties (including rice) that emerged from the Green Revolution are dominant DELLA mutants (Peng et al., 1999). Recently, Sawers et al. (2018) proposed to revisit selection for DELLAs alleles by using wild cereal varieties in order to concomitantly select for AM symbiosis, plant architectural and phenological traits. In addition, several genes encoding proteins that play important roles in beneficial mycorrhizal response such as Pi transporters or plasma membrane aquaporins are transcriptionally regulated by unknown AM signals (Fig. 3; Aroca et al., 2007; Koegel et al., 2017). A recent study where rice varieties adapted to different agrosystems (upland, irrigated and irrigated lowland) were cultivated under lowland conditions showed clear genotypic differences in terms of beneficial mycorrhizal effect (Diedhiou et al., 2016). In this study, AMF was shown to effectively infect roots of all varieties under waterlogged conditions but only improved seed production of upland rice varieties, indicating the existence of rice genetic attributes modulating mycorrhizal effects. To our knowledge, no studies have considered AM symbiosis in genetic approaches aiming at improving crop growth and productivity, by investigating mycorrhizal response in a large sequenced rice diversity panel for instance. Advances in mass AMF spore production, large scale-phenotyping technologies and association genetic techniques will allow to tackle these questions by identifying plant genetics determinants regulating AM-associated physiological mechanisms responsible for improved rice growth and resistance to abiotic stresses.

6. Conclusion

Rice consumption is continuously growing and solutions to adapt its cultivation and production to future climates are required. Among them, the use of AM symbiosis to simultaneously improve rice growth and protection against abiotic stresses is of major interest. A number of molecular determinants of AM symbiosis have been identified in rice and constitutes the basis for better understanding the physiological mechanisms leading to mycorrhizal beneficial effects, but also the environmental constrains that limits the use of AMF to improve rice productivity in agronomic environments. As reviewed here, AMF can infect rice roots in waterlogged (lowland) as well as in irrigated non-flooded and rainfed (upland) environments, where it can have beneficial effects on nutrition and seed production. However, establishment and effectiveness of AMF in agricultural soils depend on rice genotypes and rely on crop management practices (Diedhiou et al., 2016; Verbruggen et al., 2013). In particular, it would be of particular interest to investigate how AMF could further improve AWD strategies that have the advantages of reducing water inputs and rice cultivation environmental footprint while maintaining productivity. Furthermore, beneficial mycorrhizal effects on rice resistance to nutrient deficiency, salt and drought stress, as well as other environmental constrains such as heavy metal toxicity or pathogens (Babikova et al., 2013; Schützendübel and Polle, 2002), have been observed in controlled conditions. The validation of increased AM rice plants resistance to abiotic and biotic stresses in field conditions, although challenging, constitute attractive future prospects.

As part of research prospect aiming at improving rice productivity and tolerance to stresses by AMF, it appears now important to focalize research on the ecological, genetic, molecular and physiological determinants of beneficial interactions. This implies to better understand AMF communities in rice fields and its interaction with the rhizosphere microbiome in order to identify rice most compatible and ecosystem-friendly AMF (Toju et al., 2018). In addition, it requires to better understand the plant genetic factors associated with changes in hormonal balance and transcriptional reprogramming upon AM symbiosis, and the physiological signification of these changes under different plant growth scenarios. Such discoveries will constitute tools for breeders and agronomists using AM symbiosis for improving rice productivity in poor and arid regions of Asia and Africa.

Acknowledgements

Our work is funded by the Institut de Recherche pour le Développement, the Université de Montpellier, the AfricaRice and the Université Cheikh Anta Diop. We acknowledge support from the CGIAR Research Program (CRP) on rice-agrifood systems (RICE, 2017-2022). B.E.E. is supported by the Centre National de la Recherche Scientifique et Technologique of Gabon.

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